THE SPUR SHOOT OF THE PINES

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(WITH PLATES XX–XXIII AND TWO TEXT FIGURES)

Introduction

The deciduous spur shoot, with its limited growth and persistent whorled needle leaves, is the distinguishing vegetative feature of the genus *Pinus*. This structure has been generally regarded as a specialization, the more primitive form of the foliage being indicated by the single spirally arranged leaves which occur on the seedling and in some forms on the adult plant after injury. JEFFREY, however, has raised the question recently of the primitive or specialized character of the fascicled foliage of the pines in his work on the phylogeny of the conifers. He states (**15**, p. 331) that the spur shoot is "a primitive attribute of the coniferous stock" which "has persisted at least in a vestigial form, in connection with the reproductive apparatus, long after it has disappeared, or almost disappeared, in the vegetative axis of the living conifers, with the exception of the very ancient genus *Pinus*." This view is so entirely at variance with so many foliage features, in both the living and fossil forms, that it is difficult to see how JEFFREY could have "cast the balance of evidence" in favor of it. Since, however, he makes much of this spur shoot argument in presenting his case for the ancestral position of the Abietineae among the other conifers, it is desirable to direct attention at least to the most important features of the evidence which is opposed to this view. The writer (**27**) has already stated, in a brief and general way, some of these features, in a paper dealing with the relative antiquity of the Abietineae and the Araucarineae, from the standpoint of their anatomy. New material, however, has recently come to hand which has prompted this more extended treatment of the subject. The literature has also been thoroughly canvassed for information on the spur of the pines.

Of the conifers there are four genera with fascicled leaves: *Cedrus*, *Larix*, *Pseudolarix*, and *Pinus*. In the first three of these

the leaves are numerous, while in *Pinus* they are much more restricted in number, not more than 8 having been recorded up to the present. In the former, too, the number is indefinite and the leaves are spirally arranged, while in *Pinus* the definite cyclic arrangement has been established. A parallel to this is seen in the angiosperm flower, where the lower forms of both monocotyledons and dicotyledons have an indefinite number of floral parts in a low spiral, while in the higher forms the number is definite and the arrangement cyclic. The spur shoot of *Pinus* is deciduous in the second to the twentieth year (ELWES and HENRY **7,** p. 1002), and its leaves fall with it, remaining permanently attached. In the other genera it is the spur shoot which is persistent, and the leaves are cast either annually or in the second to the fifth year. The small and more or less definite number of persistent and whorled needle leaves and the regularly deciduous character of the spur shoot are features which render this structure in the pines very unlike the ordinary branch and also unlike the spurs of the other forms, which differ from an ordinary branch only in their limited primary and secondary growth. The features that will receive attention in this paper are such as indicate the branch character of the spur in *Pinus*.

Number of needles

The number of leaves in the fascicles of the pines, appearing on first sight constant, and being, as ENGLEMANN says (**8**), "the most obvious distinctive character," has been extensively made use of in their classification. He states (**8,** p. 161) that "the sections of 2-leaved, 3-leaved, and 5-leaved pines were the only ones known to the older botanists"; to these were added two other sections "by LINK (*Linnaea*, 1841), one with 2 or 3, the other with 3 or 4 leaves in a sheath." Subsequently forms with single leaves and others with 3–5 leaves in the fascicle had to find a place. Numerous exceptions to this classification have also been recorded. KRONFELD (**16,** p. 68) gives a summary of the variation in many different species observed up to the date of his article. He cites, for example, the occurrence reported by REICHARDT of 3, 4, and 5 needles in *P. silvestris*, which is normally bifoliar, and also of 3, 4, and 6 in

P. Cembra, which has usually 5 to the fascicle. To Dr. G. R. SHAW I am indebted for another reference to the 3 to 5-leaved condition in *P. silvestris* (see KIRCHNER, LOEW, and SHROETER, Lebensg. d. Blütengepfl. Mitteleur. I, 187) and for one to *P. halepensis*, a bifoliar form which may bear 3, 4, or 5 leaves (see MATHIEU, Fl. Forest, ed. 4, 608). In *Gardeners Chronicle* of 1852 (p. 693) an anonymous writer speaks of having raised a variety of *P. austriaca* (normally bifoliar) with 3 leaves. He speaks of these fascicles as being all over the tree, which was about 10 feet high and very dense. The same writer says: "I also find *Pinus Hartwegii* still halting between two opinions between a 3-leaved and a 5-leaved fir. . . . . *Pinus mitis*, *P. variabilis*, *P. muricata*, and others are too well known in their similar tendencies to need remark. My *Pinus insignis* has many a group of 4 leaves, instead of the prescribed 3." In *P. macrophylla* he found fascicles with 6 and 7 needles quite common, even some with 8. SHAW himself (**26,** p. 6), in his description of the pines of Mexico, encountered so much variation in four of the nut pines (*P. cembroides*, *P. monophylla*, *P. edulis*, and *P. Parryana*) that he said: "I find it impossible to separate these specifically, their cones being identical and the number of their leaves inconstant." The leaves in the foregoing instance varied between 1 and 5. He has also recorded (p. 23) a great variation in single species. Of *P. Montezumae* he says: "Trees bearing fascicles of 6, 7, or 8 leaves are quite common, but such excessive numbers are found usually on older trees and in favorable years. On young trees fascicles of 3 and 4 leaves may be found, but in all cases fascicles of 5 predominate." Of *P. ponderosa* the same author states that the leaves are in fascicles of 2–5, but has found fascicles of 6–8 on mature trees. *P. Teocote*, *P. patula*, and *P. Lawsoni* agree in having usually 3 to the fascicle, but the first two have occasionally 4 or 5, while this is more usual in the third. In *P. leiophylla* the conditions are evidently reversed, since SHAW (p. 13) says that the leaves are "in fascicles of 5 or of 3 and 4." SARGENT (**24,** p. 119) states of *P. serotina*: "The leaves are borne in clusters of 3 or occasionally of 4 on vigorous young shoots," while of *P. heterophylla* he says (p. 157): "The leaves are borne in crowded clusters of 2 or 3, the 2-leaved clusters being most common

on young vigorous trees and on fertile branches." In *P. Pinea*, which usually has the leaves in pairs, ELWES and HENRY (7, p. 1119) state that "on well developed vigorous branches, a few of the leaves are sometimes in clusters of threes." Of *P. Torreyana*, whose adult leaves are in fives, they also state (p. 1065) that "on young plants the leaves are frequently in clusters of 3 and 4." BORTHWICK (1) has described a tree of *P. Laricio* 12 years old with 2, 3, and 4 leaves to the fascicle. The quadrifoliar spurs were found only at the top of the tree, which was of very vigorous growth.

The variations in the number of leaves in the pines have been recorded practically as isolated instances and have not been correlated. As they stand, they show that the spur shoot is not so definite and so specialized a structure as has been supposed, but that it is more in the nature of a branch with an indefinite number of foliage leaves. When, however, one looks farther into the variations from the standpoint of the spur being ancestrally a branch, it is evident that the fascicles with supernumerary needles should be found in the more primitive parts of the plant: on the seedling, on the fruiting branch, after wounding, etc. My own investigations have been along these lines, and though they do not completely correlate the cases reported, they go very far toward doing so and afford one important line of evidence of the branch character of the spur shoot.

Fig. 1 is of the upper part of a 3-year-old seedling of *P. Strobus*.[1] Primordial leaves are unusually persistent on this plant, and may be seen among and below the three spurs with the rubber bands around their leaves. Brown scale leaves, however, replace these green seedling leaves around the base of each fascicle just as in the ordinary spur. The middle spur bears 15 leaves, the one to the right 11, and the one to the left 7. Fig. 2 is of a seedling of the same species, one year older. The main axis in this case made a comparatively short growth the last season and bears 6 fascicles. The central one of these has 9 leaves, the one to its right 10, the two below these 7 each, the lowermost to the right 5 large and 2

[1] I cannot determine absolutely that these and the other young forms are *P. Strobus*. It is possible that they are *P. excelsa*, but, since some consider the two species as geographical varieties, the matter is unimportant from the present standpoint.

small, while the lowest to the left has 6 equal-sized needles. This plant was slightly wounded a year ago last spring in connection with some work a student is doing along another line. It was not injured, however, in such a way as has been found in other cases to interfere with the number of needles. Again, several sister plants similarly injured did not show any reaction. It is probably better to consider this case a "sport," just as in the case of the 3-year-old plant, which had not been injured in any way so far as could be determined. In only one instance have I found younger plants than these with extra leaves in their fascicles; one seedling from a dozen or so of *P. flexilis*, which are now in their second year, has a fascicle with 6 needles. It is among the first formed fascicles of the seedling and at the top of the second season's growth.

It is more usual to find the spurs poorly developed when they first appear on the seedling, which is generally in its second year, though in some species they are delayed till the third year, or even later. This feature shows itself especially in species which have normally more than two leaves in the mature condition. For example, HEMPEL and WILHELM (11) refer to *P. Cembra* seedlings two years old as having trifoliar spurs, though the adult plant is normally quinquefoliate. I have also found trifoliar spurs common in *P. Strobus* when fascicles first appear on the seedling. Some spurs here are even bifoliar. In these reduced spurs the needles apparently come right out of the stem, the shoot axis, if any be present, being imbedded in the tissue. These fascicles also are usually devoid or almost devoid of bracts. In *P. silvestris* I found in 35 seedlings two years old only one example of a trifoliar spur. This was on the most vigorous of the plants. In plants a few years older, which had attained to considerable vigor of growth, I could scarcely find one without trifoliar spurs unless it was a weakling. At first the occurrence of these reduced fascicles on the seedling seemed entirely at variance with the view that the spur shoot of the pines is a branch. It is a feature, however, which is shared by other spur shoot-bearing plants. In *Ginkgo*, for example, when the spurs first appear, about the third year, they bear only 1–3 or 4 leaves, and gradually gain in number as they advance in age until

they attain their mature condition. This is also true of the other fascicle-leaved conifers, sometimes only one or two needles developing in the season that the spurs appear. There must thus be some common physiological reason underlying this feature, and no doubt it is the well known lack of vegetative vigor in the seedlings of the conifers generally. During the first few years they are busy establishing a root system and there is little stem growth. Foresters and nurserymen know this early critical stage in the life of the conifers only too well. The growth in these early years could be measured in inches, while in later years it would require feet.

I have examined older forms, 6–15 years old, of a large number of different species belonging to all the different sections of the pines, and have found supernumerary needles quite common, especially on vigorous specimens. On the main axis of one unusually sturdy plant of *P. Strobus*, a plant which had made at least a foot and a half of stem this year, and this stem fully three-quarters of an inch in thickness at its base, there was a spiral sequence of fascicles with 6, 7, 8, 9, and 10 needles. Fig. 4 is of one of these. The supernumerary needles have been surrounded by a rubber band, and it will be seen that they show a spiral gradation in length. This is a feature which to a less degree is sometimes shown by the 5 original needles themselves. It is indicative of the concealed spiral arrangement of the leaves on the spur. This feature, I find, was observed long ago by MEEHAN (**22**), and its significance noted. The series of spurs referred to above occurred on the lower part of the year's growth. It is more usual, however, to find spurs with extra needles near the apex of the season's growth. I have found many instances of this in a mixed plantation of pines about 8 years of age, which consisted of *P. Strobus*, *P. silvestris*, and *P. Banksiana*. Of the white pine there was a large proportion of vigorous specimens with supernumerary needles. The Banksian pine showed few instances, but in the Scotch pines they were very numerous. I should think fully 75 per cent of these had several (3–6 or 7) trifoliar spurs at the apex of the year's growth. These trifoliar spurs could be traced for two to three years previously at the corresponding places on the stem. The occurrence of trifoliar spurs in this species at the branch region was observed by

the anonymous writer in *Gardeners Chronicle* of 1852, to whom reference has already been made. He says of these spurs in *P. silvestris:* "I have gathered 8 or 10 examples round one bud alone," and adds "on the *macrophylla* the examples are very numerous," evidently intending it to be understood that the abnormal fascicles of this species, which he has described with 6–8 needles, were also found in the branch region. I have observed in *P. excelsa* 6–7 needles in the same position, in *P. parviflora* 6, and in *P. virginiana* 3. The first two of these are normally 5-foliate, while the third is 2-foliate. In *P. Jeffreyi*, which is normally 2–3-foliate, I have found on plants of about 8 years of age spurs with 5–6 needles; these were often in a terminal position (see fig. 13, where a branch has originated from such a spur). In all cases it is more usual for the extra numbers to appear on the main axis than on branches, though I have found them on the same plant in both places. I have examined fruiting branches in the case of *P. Strobus* and *P. excelsa* only, and have found several instances of 6-needled fascicles on these.

This normal production of supernumerary leaved fascicles, as it may be considered, is interesting, but of much greater interest is their traumatic production. The past summer, Mr. J. R. FRYER was experimenting with white pine along this line and succeeded in producing on young trees, about 15 feet high, fascicles of 6–8 leaves, in one instance 11. He cut the young growth from vigorous branches and main axes in the latter part of May, and when new growths arose they had in some cases the extra needles in the fascicles. In *P. excelsa*, at about the same height, I found in the middle of July many such cases, where the terminal bud had been injured in the early spring (probably by the pine shoot beetle, *Hylesinus piniperda*) when the fascicles were beginning to develop. The wounding caused numbers of these fascicles to develop extra leaves. Fig. 3 gives a fair illustration of the tufted appearance of these shoots and shows three fascicles with 9–11 needles (see also in fig. 10 the central fascicle). In some instances the number of leaves reached 15. In *P. parviflora* I have found on a young tree fascicles of 6–9 needles. These were near the top of the main axis, which had been slightly wounded lower down. Even in the

single-leaved pine, *P. monophylla*, wounding increases the number of needles to two. Figs. 5 and 9 are from a young tree which was normally monophyllous. Both twigs were injured just as the leaves were starting to develop. On the first, three bifoliar spurs have been produced, and on the second, one. I have not observed an increase in the number of needles by wounding in any other forms, but it is probably of quite general occurrence in the pines.

Before leaving the subject of the number of leaves in the fascicle, a peculiar and probably a specialized condition, which has been reported in several species, must be referred to. In *P. Nelsoni*, SHAW (**26,** p. 8) states that the leaves are "connate in fascicles of 3," and that this condition is found even in the seedling. In *P. Thunbergii* the leaves are in twos, while "in var. monophylla the two leaves in the cluster coalesce" according to ELWES and HENRY (**7,** p. 1143). These authors also refer to two other cases of fusion of the leaves; to CARRIÈRE'S (Conif. p. 398, 1867) description of a variety (*monophylla*) of *P. excelsa:* "each sheath with apparently only one leaf, all of the five leaves being welded together" (p. 1011), and to a monophyllous variety of *P. Strobus* described by TUBEUF in 1897, "a variety with the needles more or less cohering throughout their length, and forming a single needle" (p. 1026). It is necessary to distinguish this spurious monophyllous condition, a result of compounding, from the truly single-leaved condition in the one species, *P. monophylla*, which as MASTERS (**20**) has shown arises from the "arrested development of one of its two original leaves" (p. 126).

Scale and primordial leaves

Below the persistent whorled needle leaves on the spur shoots are spirally arranged scale leaves, which are homologous with the similarly though more laxly arranged scale leaves on the ordinary branches. They are either persistent or deciduous. On seedling stem and branches scale leaves are replaced by the so-called primordial leaves, which are a prominent feature in the pines. These seedling leaves, as COULTER and CHAMBERLAIN (**5,** p. 222) have noted, are of simpler structure than the whorled needles. There

are gradations in structure, however, between the two types of foliage. BORTHWICK (1, p. 153) refers to this feature in his description of the supernumerary needles of *P. Laricio*, to which reference has been made. He says that "the fourth needle, ... although it shows some of the primary leaf characters internally, still, in outward appearance, it resembles the normal acicular leaves, exhibiting in fact a transition stage between the two." I have found very complete series of transitions in form between both scale and primordial leaves, and also between these and the whorled needle leaves. The latter is well indicated in fig. 10, where the upper spur (5-foliate) has proliferated into a branch with primordial leaves. It is possible here to tell the spur leaves from the others only by their low spiral arrangement and by their slightly triangular rather than flat form. In the fascicles illustrated in fig. 3, some of the upper bracts have been modified into green seedling-like leaves. The needles of these fascicles, too, are flatter, shorter, and more like the primordial type. This is especially true of the needles of the fascicles in the younger plant shown in fig. 1. More definite reference to these points will be made in a future paper dealing with the internal structure. The morphological evidence, however, seems sufficiently clear that the spur shoot leaf is only a specialized primordial leaf, just as the scale leaf is also a modification of it.

The transformation to both types of foliage occurs at somewhat different stages in the life of the seedling of various pines. Of *P. monophylla*, SARGENT (**24,** p. 51) says: "primary leaves are the only ones produced during the first five or six years in the life of the plant"; while BRITTON (**3,** p. 14), in referring to this feature in *P. cembroides*, states: "juvenile leaves of this and other nut pines are produced for the first five years or more, often to the exclusion of all others . . . . the new ones shorter as the buds of the fascicled, needle-shaped leaves develop in their axils." MASTERS (**21,** *fig. 1*, p. 586) has figured the persistent primordial leaves of one of these, *P. Parryana*. He previously figured those of *P. Pinea*, a form in which he notes that they were observed long ago by LINNAEUS (MASTERS **19,** p. 258 and *fig. 8*). Of the last mentioned species, ELWES and HENRY (**7,** p. 1120) state that "the primary leaves are produced . . . . for several years, in mixture,

after the first season, with the adult geminate leaves." LLOYD'S (18) attention was attracted to the great persistence of the primary leaves of a young plant growing in the New York Botanic Gardens. In *P. canariensis* the leaves persist even longer than in *P. Pinea.* In *P. rigida* they are also very persistent. In the seedlings of most forms, however, the primordial leaves do not last beyond the second or third year.

Primordial leaves are not, however, restricted to the seedling. According to MASTERS (**19,** p. 258), "they occur frequently on the lower part of the shoots of the year, as in *Pinus sabiniana*, *Pinea*, *silvestris* (sometimes), and other species"; also "in some cases, on the branches or stalks immediately supporting the cones, as in *Pinus excelsa*, etc." In *P. monophylla*, ELWES and HENRY (**7,** p. 1056) have noted that "in cultivation adventitious shoots bearing flattened primordial leaves are occasionally produced on the lower branches." SHAW (**25,** p. 206), in speaking of the "summer" growth of certain southern pines of the United States, says: "this growth, in the summer, differs from the spring growth not only in its less development, but also in its *green* bracts, which, not being required for the protection of the winter bud, assume more or less completely the size, color, and character of the primary leaf." SARGENT (**24,** p. 4) states that: "*Pinus rigida* and *Pinus echinata* are the species of the United States which generally bear primary leaves on branches, or produce freely shoots from the stumps of cut trees. These shoots, which are clothed with primary leaves, grow vigorously for a few years, and then usually perish." ENGELMANN (**8,** p. 163) speaks of this feature in *P. inops*, *P. rigida*, and *P. canariensis*. In the last mentioned, it is very prominent in some instances. Miss COOLEY (**4**) refers to and figures a tree at Naples which was practically clothed with shoots bearing primary leaves. A young specimen of the same species in the New York Botanic Garden shows many reversions to primary foliage. Whether in these instances all the reversions may not be the result of injury is uncertain. Wounding does give a response in the case of the production of resin canals for several years after the injury, especially prominent being the response in young twigs which are formed subsequently to the wound, and it is probable

that the extent of the primary leaves due to wounding is much greater than at first appears.

The possibility of reviving the primary type of foliage by wounding must be fairly common in the pines, for in addition to the ones that have been mentioned, MASTERS (**19**, p. 258) refers to their production after injury in *P. edulis*, *P. Parryana*, and *P. Khasyana*. The past summer I have observed it in ten or more species: *P. canariensis*, *excelsa*, *halepensis*, *Jeffreyi*, *Laricio* and var. *austriaca*, *monophylla*, *Pinaster*, *Pinea*, *ponderosa*, *Thunbergii*, and *tuberculata*. LLOYD, moreover, has produced the primary type of foliage experimentally in *P. ponderosa*. He states (**18**, p. 101; see also original article, **17**) that "shoots, which normally would bear only thin, brown, papery scales, namely the shoots which bear the male or pollen-bearing cones, may be made to produce true primordial leaves by the mere pruning away of the upper part of the shoot early in the spring." HOCHSTETTER (**12**) has gone farther, and has succeeded in fixing the juvenile foliage in *P. Pinea* and *P. canariensis* by cuttings, having accomplished in this specialized genus of the Abietineae what is common practice in the Cupressineae. He states (p. 367): "Stecklinge von *Pinus canariensis* und *Pinea*-Sämlingen, im zweiten oder dritten Jahre abgenommen, wachsen leicht an, verharren in der Primordial-form und bilden bläulich-grüne Büsche mit spiralig einzeln gestellten Nadeln von unvergleicher Schönheit." Unfortunately, these "incomparably beautiful" shrubs are but short-lived. Had they succeeded better and become disseminated through horticulture, they would have afforded a convenient and valuable demonstration of the primary type of foliage of the pines.

In some seedlings of *P. Strobus* in the third year I have found a reversion to primordial leaves where no wounding could be detected. The leaves, for example, shown on the branch above and to the left of fig. 11, though broader and more closely set than usual, are primordial leaves produced after the plant had formed spur shoots. Such leafy branches may even originate from a spur shoot, three stages of differentiation being shown in the figure. To this point, however, reference will be made again. MASTERS has observed (**19**, p. 258) in *P. rigida* and *P. silvestris* that if the main axis is

injured slightly above the cotyledons the branches which are produced in response to the wound bear only primordial leaves. He considers that this doubtless occurs in many others. From these facts and the stump sprouting, which has been referred to above, it seems probable that in all cases the epicotyledonary region, in the young plant especially, reverts more readily to the primordial type of foliage than the upper parts of the stem, and that what seems more or less normal here and, in some cases below the cones, can be made to occur in other parts by wounding. PHILLIPS (**23**) has recorded some observations bearing on this point. Speaking of the sprouting of *P. chihuahuana* after injury by cattle and fire, he says (p. 385): "typical sprouting . . . . is confined to trees under 5 cm. in diameter (measured at breast height), which send up most of the shoots from the root collar or the first 30 cm. above ground." This power of stump sprouting, as it is called, also decreases with the size of the stump: "Not a single case was found where the stumps of trees smaller than 7.5 cm. in diameter had failed to produce thrifty sprouts, and fully 30–50 per cent of the stumps of trees up to 22.5 cm. in diameter had produced very thrifty sprouts, most of the fail stumps occurring between the 15 and 22.5 cm. classes" (pp. 386–387).

Proliferation of the spur shoot

The spur shoots, like ordinary branches, arise either in the axils of primordial leaves or, when these have been replaced on the stem by scale leaves, in the axils of the latter. Unlike the branch, however, the spur shoot of the pines increases neither in length nor in diameter after the first few weeks, though it may remain on the tree with leaves green and apparently functional for many years. Thus, primary meristem and cambium are normally inactive through by far the greater part of the life of the spur shoot. This limited growth of the spur shoot and the production by it of only one set of assimilatory leaves which are persistent, not even detached on the fall of the shoot, are the distinguishing features of the spur of the pines. In the other fascicle-leaved conifers, a new set of leaves is added to the spur shoot each year for many years (cf. *Ginkgo*). There is thus a slight annual increase in length, the

spur shoot elongating, much after the fashion of the cycad stem, enough to accommodate each new set of leaves. The "spurs" in these forms may attain a length of an inch or more on the older branches; they gradually become shorter toward the younger parts, and on the season's growth primordial leaves alone may be present. These persist in *Cedrus* for two to three years. The occurrence of these primordial leaves on the season's growth are a contrast to the condition in the pines, where only scale leaves are normally produced. In *Cedrus* the fascicled leaves themselves persist for two to five years, while in *Larix* and *Pseudolarix* they are shed annually. In the pines they are indefinitely persistent, falling with the spur. Undoubtedly the persistent habit is the ancestral one for the conifers, having been overcome in two ways, by the deciduous leaf and by the deciduous branch, as the writer has tried to show in a recent article on the Araucarineae (27).

The spur shoots of the three genera referred to, in addition to having the power of making a short yearly increase in length, have also the power to a marked degree of forming ordinary branches as occasion arises. The main axis may originate from a spur shoot, usually the terminal one, but if this is injured, any of the proximals may assume its function. Lateral branches also arise normally from spur shoots, especially from the younger ones. When, however, a branch is injured, they may arise from old spurs. The spur shoot of these three genera retain to a marked degree the power of branch formation. It remains, however, to a large extent latent unless called into activity by the needs of the plant. This dual power of the spur shoot either to produce a branch or to continue the growth of the fascicle as such is an indication of the genetic relationship of the branch and spur shoot. One would scarcely expect such a feature in the pines, where ordinarily in the mature condition not even a rudiment of a bud can be discerned amid the closely set needles of the fascicle, and where, too, only the one set of leaves is produced and the axis neither increases in length nor in diameter after it has formed these.

On the contrary, however, proliferating spur shoots similar to those in the other genera are of very general occurrence in the pines. They do not occur so abundantly nor so normally as in

the other genera, and have escaped observation to a great extent. Several instances, however, are on record. ENGELMANN (**8,** p. 167) says: "in exceptional cases and as a monstrosity the leaf bundles may become proliferous, the branchlet which bears the secondary leaves elongating and forming a regular branch." MASTERS (**19,** *fig. 9* and p. 267) figures a pine, with two needles, in which the fascicle is "prolonged into a shoot with primary leaves and leaf buds." Neither ENGELMANN nor MASTERS mentions the species concerned, nor in either case do they indicate the conditions which have induced the proliferation. DICKSON (**6**) and MEEHAN (**22**) both observed that in *P. silvestris* proliferation occurred as a result of injury. DICKSON's specimen was a twig, the extremity of which had been destroyed. He says (p. 260): "the development of these buds is stronger the nearer their position to the seat of injury." The lower ones are merely closed buds, but the upper ones "develop well marked foliage leaves, and, in the very strongest ones, these foliage leaves have secondary bifoliar spurs developed in their axils." In the development of foliage leaves spirally arranged "on the prolonged axis of the stimulated spur," DICKSON notes "a reversion to the early or unspecialized condition." MEEHAN'S (**22,** p. 82) specimens were Scotch pine that had been "headed back." Previous to his observation of these proliferating spur shoots, he had been so influenced by VON MOHL'S work on *Sciadopitys* that he was inclined to consider the fascicled needles of the pine as cladodes. He now subscribed to the current view and recognized that the whorled needles are leaves and that the fascicle is an "arrested branch, having a dormant bud at the apex." BORTHWICK (**2**) has observed numerous instances in a plantation of *P. Laricio* and *P. silvestris*, and has studied the conditions under which they develop, as well as the character of the resulting branch. He considers that "the interfoliar bud develops only under the stimulus of an increased supply of nutriment," and instances several kinds of wounding which result in a greater advention of food material. In this he agrees with HARTIG'S explanation of the development of dormant buds. He considers that the branch produced from the development of the interfoliar bud may bear either primary or fascicled leaves, "the results

varying with the conditions under which the buds are induced to develop and the general health of the tree at the time" (p. 157); the greater the supply of nutriment, the more likely it is that the proliferating branch will produce spurs, the primordial foliage occurring on those with the smaller supply. BORTHWICK has even referred to an economic aspect of the proliferation of the spur. He considers that the appearance of scraggy pine trees could be improved by a judicious disbudding process and a stimulation of the spurs to form branches.

It is in the seedling and in the young vigorous plant that I have observed most instances of proliferation, the occurrence of proliferating spurs following very closely that of supernumerary needles. This applies also to their common production in the mature tree by wounding.

The upper part of a seedling of *P. Strobus* at the beginning of its third year is shown in fig. 6. A branch with young spur shoots (this season's growth) has been developed from the interfoliar buds of four spur shoots of last season's growth. The central one of these will probably form the future stem. The big branch to the lower right of the photograph, whose leaves have been tied together, arose a year previously also from a spur. Above it is a normal fascicle which has not proliferated. The main axis below the leafy part had its end destroyed, as its dead stump shown against the small white slip indicates. Its lower branches, which were uninjured, bore only normal spur shoots, and it is possible that wounding has had something to do with the proliferation of the upper spurs. I found, however, in what so far as could be determined was an uninjured sister plant, one case of proliferation. In another, also apparently uninjured, I found a reversion to primordial leaves, which has been previously mentioned; though the large branch shown to the upper left of fig. 11 did not arise from a spur shoot, at least, if it did, no trace of the fascicle of leaves remains, yet to the right of the terminal bud there is a spur shoot with a small set of primordial leaves, while to the lower left of the figure two other fascicles are shown with smaller series, so small that they are practically green buds. This photograph was taken while the plant was in its winter condition. Two of these fascicles have since

developed into branches with both primary and secondary leaves. I have found similar proliferations on seedlings from the same plot, but could detect no injury except in one instance. The seedlings were all grown and carefully tended in the University Garden. Moreover, in both seedlings shown in pl. XX there are well developed buds in all the spurs except two (the lowermost of fig. 2), some of which will in the ordinary course of events grow next year into branches. In fact, the main axis will come from one of these in both instances, as it has done in the plant shown in fig. 6. One is so much larger than the others in each case that there seems no doubt of its power to produce the main axis.

On examination of older seedlings of other species, I found that branches had quite frequently arisen from spur shoots in certain plants, again not connected with any apparent injury. Among about 20 young plants of *P. virginiana* (?), several had proliferating spurs, and were vigorous specimens about 6 years of age. In fig. 7 the two leaves (marked with a single line each) inclose the terminal axis with a rosette of lateral buds at its apex. These two leaves have very broad bases. Below and to the right is a lateral bud coming from a spur shoot with three leaves (marked with 2 lines each). Two of these are also broad, but the third is much narrower. It is to be noted that this species has its leaves normally in twos. Below this spur shoot is one with two broad leaves (marked with 3 lines each) and a much smaller bud, below which again are spur shoots with smaller and smaller buds, until at the base of the shoot figured no trace of a bud could be discerned, even with a lens. During previous years certain of the branches also arose from spur shoots on this plant. In vigorous specimens of *P. Strobus*, about 8 years of age, chiefly from the plantation referred to before, but in the wild also, I have found that usually subsidiary branches occur below the normal whorl. These are smaller and in almost every instance derived from the proliferation of a spur. One of them at the end of its first season's growth is shown in fig. 8. It has normal secondary needles and is only one of several at the same node. Around the apex of the stem below the branch node, a number of this year's spurs have small buds which are ready to develop next year into similar branches. In a few specimens of

P. parviflora, I found numerous examples of similar proliferations. A large proportion of these branches formed in this way perish later, but some persist and develop normally. Sometimes in these species the spurs which will proliferate have an extra needle. In *P. silvestris* this is normally the case. In vigorous specimens the lower branches on the swollen branch node of this form come regularly from trifoliar spurs. Many of these branches persist, and I have also observed that sometimes the main axis comes from a spur, no special terminal bud being formed. This condition, however, is rare in the Scotch pine at the stage (about 8 years old) examined. In *P. Banksiana* in the same plantation proliferation was not so common as in the other two species,[2] but occurred under the same conditions.

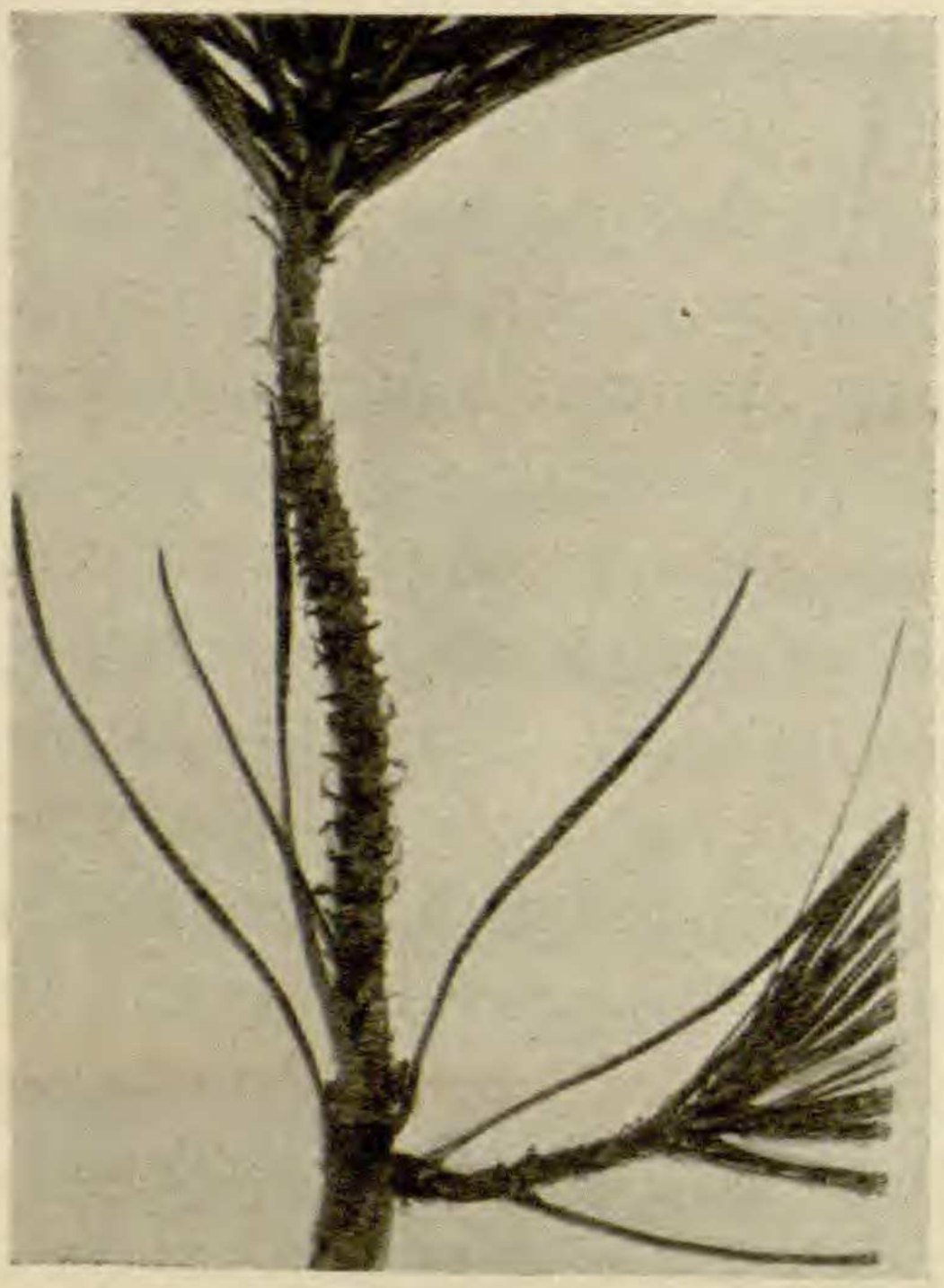

FIG. 1.—*Pinus ponderosa* var. *Jeffreyi* (one-half nat. size): the main axis and a branch developed from spur shoots in a plant about 6 years old.

In some young plants of *P. ponderosa* var. *Jeffreyi*, I have found proliferation very common. These plants were about 6 years of age, and did not exhibit any special vigor of growth. Text fig. 1 shows the main axis and a branch, with some of the needles of the spur from which they arose attached to their basal regions. Others of these needles have become detached. In these plants there are normally only 3 needles to a spur. In the axial stem-producing spur shown above, 4 needles are still attached to the base, and the broken stumps of 2 others can be clearly seen. The branch spur has but 2 needles intact, but the stumps of 2 or 3

[2] Mr. C. H. MORSE, while on a visit to the government nurseries in Norfolk County, was good enough to examine Scotch, Banksian, and white pine, and reports that "proliferation is very abundant, especially in vigorous plants of *P. silvestris* 6 to 8 years of age, and fairly common in *P. Banksiana* and *P. Strobus* of about the same age."

others can be made out on the specimen, though not in the photograph. When one examines the insertions of these needles, they are seen to continue the spiral series of the scales above them, which are more developed than usual and more than usually persistent.[3] The spiral is a very low one in the case of the 3 lowest (the normal) needles, but comes out clearly in the supernumerary needles. In these, too, there is a very evident gradation in length, the leaves getting shorter the higher they stand on the axis. In fig. 13, for example, the 3 large (slightly spirally twisted) needles, though each is inserted at the base of a spiral series, are all about on a level. The other 3, however, are inserted at quite distinct levels. The shortest is the highest, the variation in their length being an inverse index of their position on the stem. This is true of the supernumerary needles of *P. Strobus*, shown in fig. 4, though their relative postions are not indicated. It is very noticeable in *P. Jeffreyi* that it is the spur with the supernumerary needles that proliferates most freely, though sometimes normal fascicles do also.

In general, the needles of fascicles which have proliferated are irregularly deciduous, remaining attached for a good while usually, and often becoming brown and weathered. One can often detect spurs that have proliferated by these needles. I have seen these needles persisting in the Scotch pine when they had become separated as much as three-quarters of an inch by the expanding base of the branch. This forces on one's attention the thoroughness with which the secondary as well as the primary meristems of these fascicles have been revived, the pines in this respect showing complete agreement with the well known condition in the other genera of fascicle-leaved conifers, where, however, normal proliferation is much more abundant. It is significant that normal proliferation in the pines occurs in the branch region of the stem and from fascicles with extra needles or in association with such fascicles.

Only in the seedling have I ever observed that the branch arising normally from a spur bears primary leaves. After injury, however, this is of quite frequent occurrence, especially on young plants. The branch coming from the spur in fig. 10 of *P. excelsa*

[3] Though I did not see these in the young condition, I should infer that they were then green.

has very long green bracts near its base and shows the gradation between fascicled and primordial leaves, to which reference has already been made. I have also found green bracts on the branches from spurs of *P. excelsa*, *P. halepensis*, *P. Jeffreyi*, *P. Laricio*, *P. Pinaster*, *P. Pinea*, *P. Thunbergii*, *P. tuberculata*. These are especially large in the *P. Thunbergii*. I have also observed ordinary proliferation due to wounding in *P. resinosa*, *P. silvestris*, and *P. Strobus*. In most cases these were young trees about 10–15 feet high. In the case of *P. Laricio*, *P. Laricio* var. *austriaca*, *P. resinosa*, *P. silvestris*, and *P. Strobus*, the trees were mature.

In fig. 12 two proliferating bifoliar spurs from an adult Scotch pine are shown. It will be noticed that they are the two uppermost spurs (cf. DICKSON'S observations cited above), and that the injury was done to the apex of the shoot of the year when the little spurs were just developing, not more than one-half an inch in length (see the one attached to the dead apex of the main axis). This is a feature which is usual in other species as well. When the injury is done to the terminal part of the young developing shoot, I have always found a proliferation of the spurs below the injured part. This never extends to the needles of a previous year, nor have I observed that a spur shoot bud can ever be revived after it has remained dormant over the winter, unless some preliminary growth took place the first year. This feature, however, is being investigated by Mr. FRYER, who is carrying on a series of wound experiments on the pines in order to determine at what season, on what year's growth, etc., the best proliferation can be obtained by wounding. He has not found that in the mature tree the spurs of *P. Strobus*, when a year old, can be induced to develop, though those of the season's growth do so very abundantly if wounded early. His test cases were with twigs which had proliferated last year. He tried to arouse the dormant buds of neighboring fascicles by cutting away all but the lowest and smallest of the proliferated spurs. Only those that had grown the year before showed any signs of doing so this year. It seems probable, then, in this species that when the bud of the spur has lain dormant over the winter it cannot be revived. The leaves in this form are shed in the second year, and whether or not those with more persistent spurs can be

made to proliferate after they have undergone one or several winter resting periods has yet to be determined. According to my own observations, it is much easier to induce a young vigorous tree to proliferate than an old slow-growing one, early wounding of the tip of the bud of the season being most effective.

General statement and conclusions

The lack of definiteness in the number of leaves in a fascicle, and the occurrence of supernumerary needles in the recognized primitive region and after wounding, are evidence of the branch character of the spur of the pines. The normal occurrence of single spirally arranged leaves in the seedling, their appearance at times on the cone-bearing branch, their traumatic revival in many instances in the adult, and the transitions which have been found between them and both scale and fascicled leaf, practically demonstrate that ancestrally the leaves of the pines were spirally arranged on ordinary branches, and that the spur is derived from this condition. Its normal proliferation in the seedling and young plant into an ordinary branch with both primordial and fascicled leaves and the traumatic revival of this condition in the mature tree place this conclusion beyond reasonable doubt. In all these features the pines differ from the other spur shoot-bearing conifers only in degree, in conformity with their more specialized condition. If in the one case the spur is a branch, it certainly is in the other. The pine spur shoot, moreover, is wholly vegetative, while in the other forms it is less specialized and combines both the vegetative and the reproductive functions, as is the case in *Ginkgo*, the most primitive of our living spur shoot-bearing forms.

When one comes to compare the conditions in the living pines with their fossil progenitors, several important points develop, which bear out the branch character of the spur. FONTAINE (9) has described several species of pines from the Potomac or Younger Mesozoic, having had to modify HEER'S genus *Leptostrobus* slightly for their reception. These remarkable pines had needle-shaped leaves "scattered on the larger or principal stems and grouped in bundles on the ends of short twigs" (p. 227). Some of the fascicles from FONTAINE'S work are reproduced in text fig. 2. They bore

more needles than any pine of today does normally, but in this feature and in the fact that they have considerable axis supporting them they remind one of such fascicles as those of *P. excelsa* (fig. 3), which were produced after bud injury. The fascicles of the fossil form, too, are described as terminal as well as lateral, and must have grown out into branches and the main axis, just as has sometimes been observed in the living pines. The lack of differentiation, too, between the primordial and fascicled leaves and the persistence of the former on old branches afford a full explanation of the transitions which have been found between these leaves in the living pines and also of the occasional "revival" of primordial leaves on old trees. In fact, no better "generalized type" could be desired for the ancestors of the pines than FONTAINE has described. Two other fossil forms have also significant features. In *Prepinus* of the Cretaceous, whose discovery we owe to JEFFREY (14), the spur shoot has 20 or more leaves. These leaves are not cyclic, but are spirally arranged, and are stated to be subject to considerable variation in number. This spur shoot is nothing more nor less than a small branch with closely set leaves, very similar to the condition described in the seedling of certain pines and in the adult after injury. This spur is apparently deciduous, however, but JEFFREY (15) has described one from the Triassic (*Woodworthia*) with very persistent spur shoot, remaining 50 years or more attached.[3]

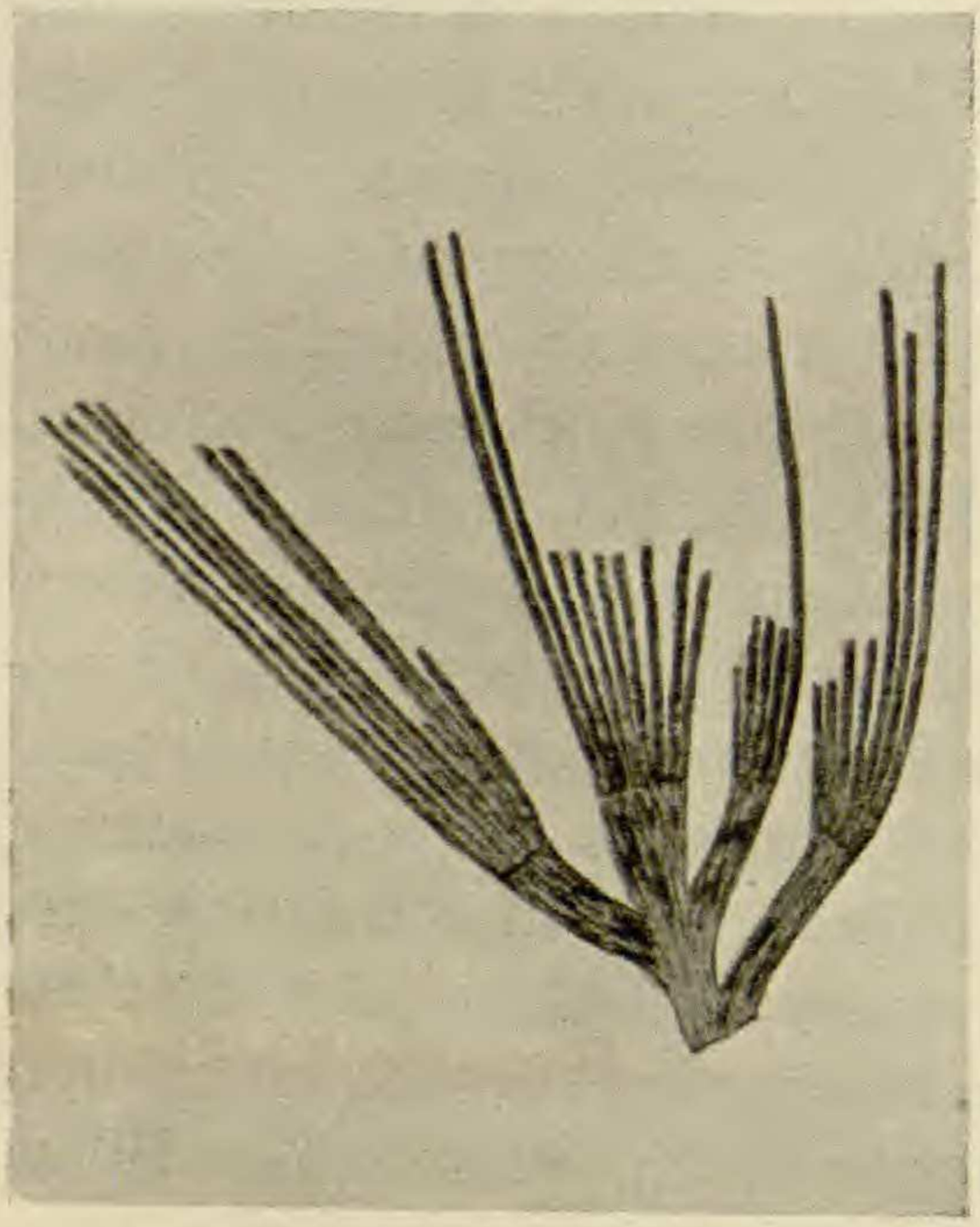

FIG. 2.—*Leptostrobus longifolius:* from FONTAINE (9, *pl.* 102); reduced one-half.

[3] It is recognized that JEFFREY considered this form a pine specializing in the direction of the araucarians and not as an ancestor of the pines and their allies. Since, however, it has been recently shown that no authentic abietinean forms have been described in the strata prior to it (see GOTHAN 10 and THOMSON AND ALLIN 28), this form must stand as the ancestor of the pines and their allies until some other fascicle-leaved conifer displaces it.

This is certainly a very branchlike feature, and it is noteworthy that it occurs in the most ancient spur shoot-bearing conifer on record.

The paleontological evidence afforded by the fossil pines supplements that from the living forms, and makes the case for the specialized character of the spur shoot of the pines practically complete. The spur then, as it stands today, is only a specialized branch which is of limited (primary and secondary) growth and bears a limited number of specialized and cyclically arranged leaves; whereas its progenitor, judging from the adult living and fossil forms and from the seedling and traumatic phenomena above described, was an ordinary branch. If such is the case, the genus *Pinus* is a specialized one in respect to its fascicled foliage, and the spur shoot of the pines cannot be the indication of primitiveness which JEFFREY'S statement, quoted in the introductory paragraph, would lead us to expect. According to it, the fascicled condition of the leaves is "a primitive attribute of the coniferous stock." This condition, he considers, has been retained in the cone of all, but "in the vegetative parts of only the very ancient genus *Pinus*." It is not apparent why *Pinus* is singled out for this distinction and not some of the other spur shoot-bearing conifers, or *Sciadopitys* whose cladode is recognized by all adherents to the "brachyblast" theory of the cone structure as the closest approximation in the vegetative parts to the condition in the cone scale. Moreover, JEFFREY, in stating the arguments in support of his view, puts much emphasis on the homology of the cone structure of the living and cordaitean forms (**13**, p. 23). The latter, he, in common with many other anatomists, regards as the ancestors of the conifers. If JEFFREY'S inference that fascicled leaves are ancestral for the conifers because of the brachyblast structure of the cone, be applied to the cordaitean forms the logical conclusion is that they must have had their leaves in fascicles. Of this there is not a vestige of evidence. All that the "brachyblast" theory postulates in this regard is the power of branching, a feature which is common to both Cordaitales and Coniferales. If, moreover, the spur is "a primitive attribute of the coniferous stock," we should expect some indication of this in the primitive regions of the non-fascicled conifers; in their seedling, on their fruiting branches, as a result of

wounding, etc. There is no more evidence of this than of fascicled foliage in the cordaitean forms.

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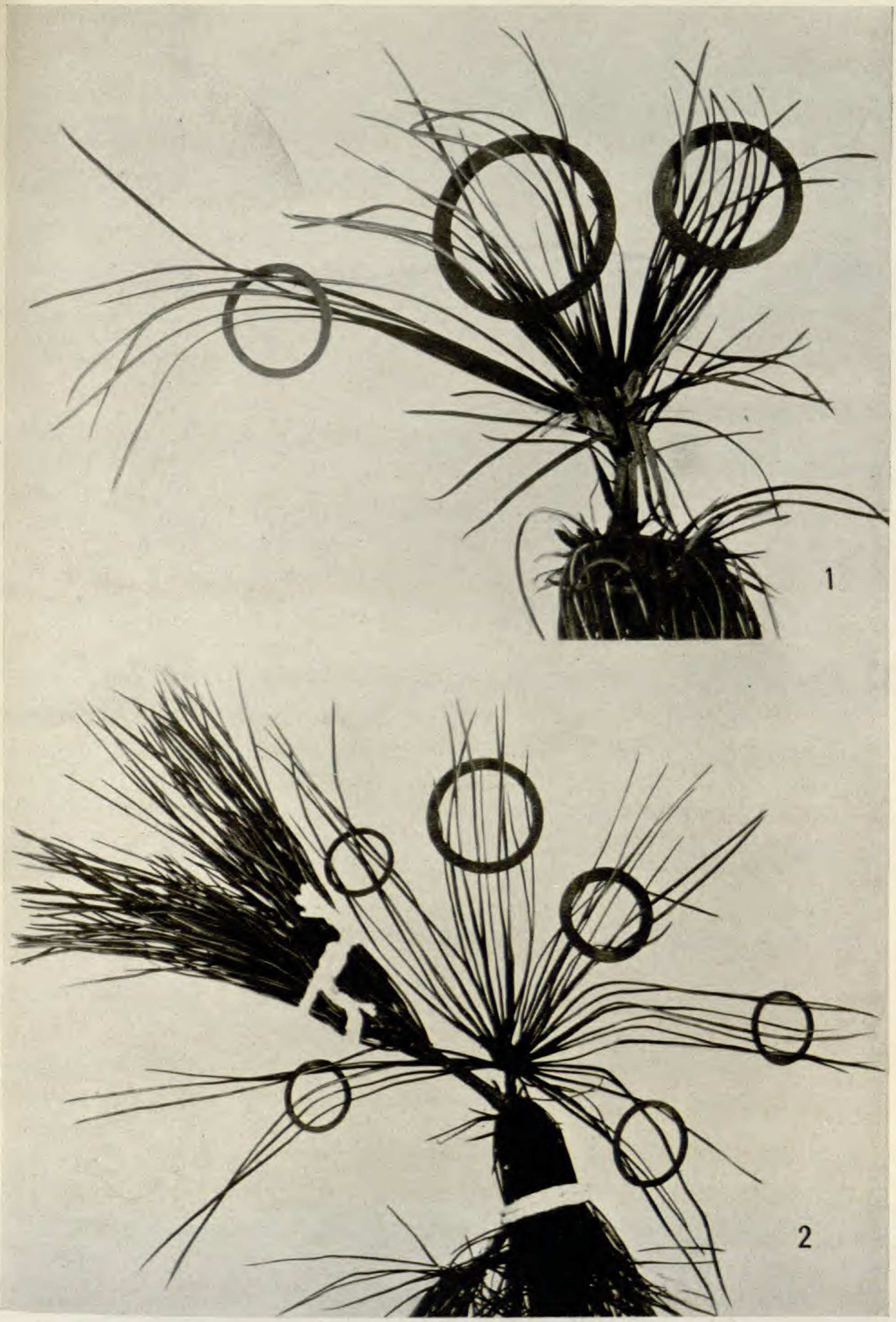

THOMSON on the SPUR SHOOT